SEASONAL CLIMATES AND FLOWERING TIME

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ABSTRACT

A study of the flowering times of plant species in Kings Park and in the hills around Kalamunda has made it possible to correlate these times with the average seasonal variations of several climatic elements: daylength, global radiation, ultraviolet radiation, atmospheric ozone, temperature, dew days, rainfall. Great caution is needed when correlating these strongly seasonal data. The finding of strong negative correlation between ultraviolet radiation (UVR) and flowering may be very significant. Slight differences in flowering time were found according to the main colour of the flowers, and (for introduced species) according to geographical origin.

INTRODUCTION

Publication of the very interesting and informative paper by Bennett (1995) on the plants of Kings Park coincided with the publication of the beautiful field manual on the wildflowers of the West Coast Hills by John Marshall and members of the Darling Range Branch of the Wildflower Society of Western Australia (Marshall *et al.*, 1995). Both works contain lists of plants with their months of flowering. A comparison of the data listed may add further interest. The timing of flowering in relation to the season's climate appears worthy of some study.

The Bennett paper distinguishes between species native to Kings Park and species naturalised there, but does not give the actual region of origin of the latter. This leads to unexpected results just because of the strict accuracy of the criteria followed. The most extreme example is that of the Geraldton Waxflower (*Chamelaucium uncinatum*) which is listed as naturalised in Kings Park because it does not occur there naturally. On the other hand its southernmost natural occurrence is in a very similar environment at Bold Park, only a few kilometres away. The yellow-flowered Evening Primrose (*Oenothera drummondii*) comes from Texas, the Field Poppy (*Papaver rhoeas*) and many other field plants from Europe. The Arum Lily *Zantedeschia aethiopica*, the Baboon Flower *Babiana stricta*, *Freesia* sp., *Watsonia* spp., *Pelargonium capitatum* and several other garden species and the unwelcome Veldt Grass *Ehrharta calycina* come from South Africa, which has diverse climates. Many escaped garden species and practically all escaped field species usually grown for food or fodder have been subject to selective breeding and their response to the climatic environment may have been affected and probably reduced.

The Marshall *et al.* book includes all plant species flowering in the Kalamunda Shire. The number of naturalised species is smaller than in Kings Park. On the other hand the species listed have been separated by the prevalent colour of the flower. As defined in the book, white includes cream and other off-white shades, yellow includes orange, red includes pink and lilac, blue includes purple. A category "other" include mixed colours, brown, bronze, greeny-brown (which could all be grouped under brown), but also green and grey-white. This broad classification by colour allows the introduction of an interesting point of view, as shown by the significant differences which are discussed further and are illustrated in Fig. 8.

DEFINITION AND LAG OF BASIC CLIMATIC FACTORS

Climatic records are kept by the Bureau of Meteorology, and monthly averages for the most frequently used climatic elements have been published in metric units. Some other mean monthly data from other Bureau publications have been assembled and converted to metric units (Gentilli 1971). Solar radiation data are taken from Spencer (1976). Measurements of ultraviolet radiation were discussed and shown by Gies *et al.* (1994).

The length of record varies considerably, from the longest period (for the amount of rainfall, from 1876) to the shortest periods of only a few years for low cloud and some wind data, and one year for ultraviolet radiation. As to the flowering time, some plant species probably combine a long-term response to the climatic stimulus now already part of their genetic make-up, with a short-term response to marked climatic aberrations, such as an unusually long drought. To study the latter phenomenon one would need separate observations of flowering times from each month in each year, and the corresponding climatic data. The biological part of this database is the essential part of phenology and is still not available at present, with the exception of some agricultural data, notwithstanding its having been advocated nearly half a century ago (Gentilli 1949).

A note of caution is needed. Solar radiation data, and consequently temperature data in all except sub-equatorial latitudes, are subject to a very distinct seasonal rhythm. With the same exception, the flowering cycle of plants is also subject to a strong seasonal rhythm. Therefore, very close statistical correlations between monthly climatic data and monthly flowering of plants need not necessarily result from a cause-and-effect relationship and may be due to a simple similarity of rhythm or concomitance in more or less parallel series of monthly data.

The study of these correlations is also complicated by the fact that, since flowering is a complex physiological activity of the plant, a certain time may have to elapse between the climatic stimulus and the actual flowering. This time delay or *lag* may be minimal for the proverbial mushrooms and very long indeed for

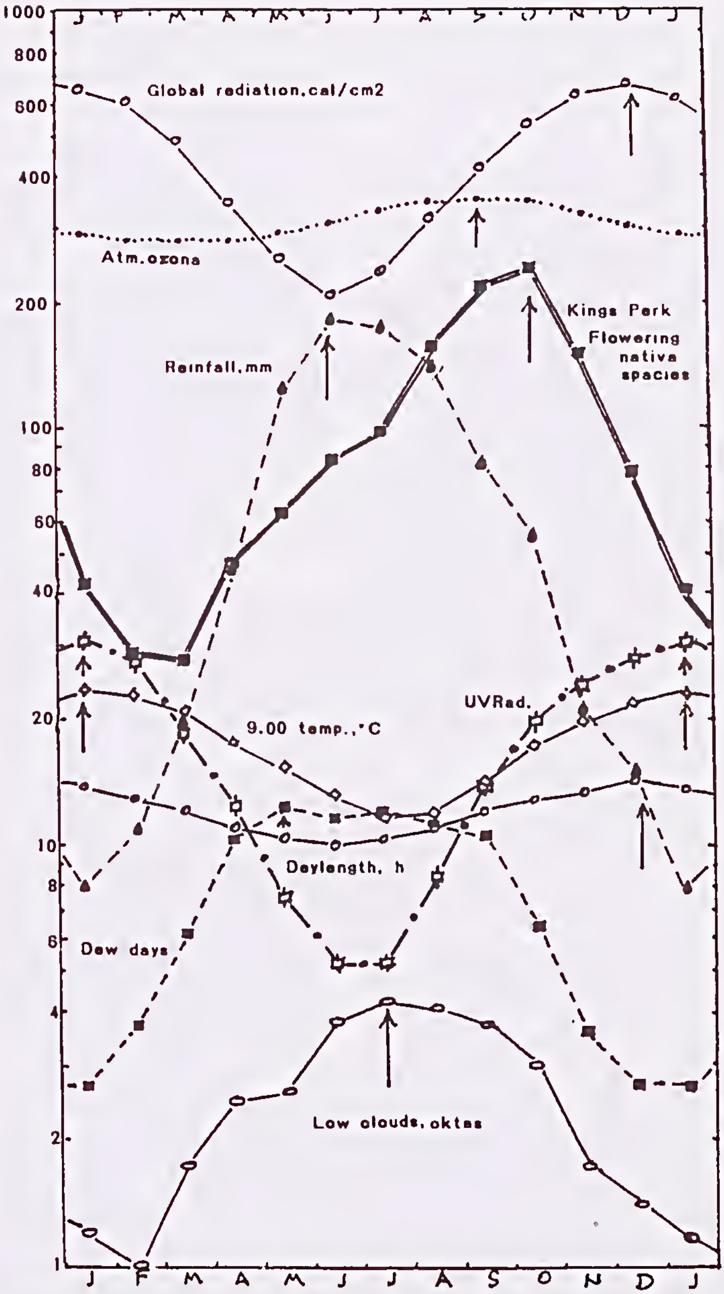

Figure 1. Some typical climatic elements for Perth, W.A. The arrows show the highest monthly value. The double line shows the monthly number of plant species flowering in Kings Park: notice how, especially in its rising section, it lags behind the graphs of climatic elements.

large trees. Fig. 1 shows monthly averages of some of the climatic elements most likely to have some significant effect on flowering time. The graph shows these averages on a logarithmic scale in order to fit data which, according to the units used, range from hundreds for solar radiation, ozone and rain (at the top) to just over 1 for low-cloud cover in summer (at the bottom). A great advantage of the logarithmic scale is that equal rates of change (here, from month to month) are shown by equal slopes. On an ordinary (arithmetic) scale a doubling, say, from 100 to 200 would look enormous, while a doubling from 1 to 2 could hardly be detected. Fig. 1 thus shows clearly the different *rates* at which the various climatic elements progress throughout the year. It also shows, of course, which elements peak in winter and which ones do so in summer, also, which ones have a steep and sharp or a low and shallow peak.

An added complication, which shall not be studied here and on which there is a most extensive literature, is the effect of *cycles*, from the obvious cycles in species with a biennial lifespan to the more subtle ones of many perennial plants, besides of course the elusive cycles in climatic events.

Since, as shown in Fig. 1, all data are represented by curves based on monthly numbers, any statistical analysis can only show how closely the various curves resemble one another. The closeness of the resemblance between any of these curves may be expressed by r or R, the coefficient of correlation (or regression, as it was originally called). R ranges from 0 (no resemblance at all) to 1 (identical). R^2, the square of the coefficient R, which drops much more rapidly from 1 to 0, is much more reliable. Adjusted R^2 is further reduced version of R^2 to allow for the smallness of the sample, in this case only the 12 monthly data. SE is the standard error which might be expected when calculating y (here, the number of species in flower in a given month) from the value of x (any climatic factor for the same month). The often extraordinarily small values of p here express the probability that the close similarity between the curves examined may be due to chance; it must not be taken as a measure of any other relationship.

THE EFFECT OF RAINFALL ON FLOWERING TIME

The native plants from Kings Park, which constitute a geographically more homogeneous population, will be examined first. The double line in Fig. 1 shows the number of native species in flower in each month, from a minimum of about 20 in February–March to a maximum of some 220 in September–October. As the slope of the line shows, the rate of climb from the summer minimum to the spring maximum, taking 6 months, is much slower than the 4-month drop from the spring maximum to the following summer minimum.

It is a general principle that, where a necessary climatic element is in short supply, plants are much more sensitive to it. A thorough examination of the temperature relationships of plants was already due to De Candolle (1855). Schimper (1898) quoted experiments which showed that, other things being equal, drier conditions tended to induce flowering, while increased watering tended to reduce it. In Western

Australia temperature (except for damage by extreme heat) is not a limiting factor, but rainfall is. Fig. 1 shows that the climatic element with the most similar (but much more symmetrical) seasonal pattern to that of flowering time is rainfall. However, if the number of flowering species in any month were plotted against the rainfall for the same month one would obtain the pattern shown by the small circles, dashed line and cursive letters in Fig 2. No strong trend can be seen in the straight dashed line which runs nearly horizontally from March (near left) to June (far right). Proceeding anti-clockwise, from July to October (highest point on the graph) the rainfall decreases while more and more species blossom. In October–November the lag decreases, and throughout the summer it remains minimal.

The two graphs (rainfall and flowering time) in Fig. 1 show that flowering time lags behind rain by about 2 months in summer, and falls further behind until the lag grows to over three months at the peak of the winter rains. This lag persists at about three months throughout the autumn. In practice it will also vary slightly according to climatic fluctuations that may occur from year to year, and of course to the adaptation and tolerance of the plants as species and as individuals.

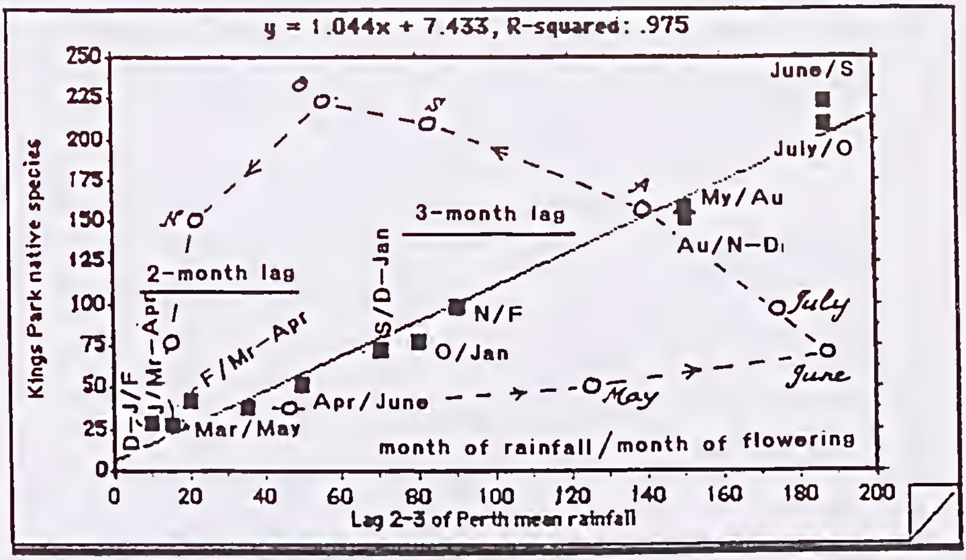

Figure 2. Correlation between mean monthly rainfall and number of native plant species blossoming in Kings Park. The small circles and cursive letters along the dashed line show total rainfall and flowering plant species for each month, in an anticlockwise sequence because the correlation is positive. There is almost no correlation from January to June (near-horizontal line), and a strong seasonal cycle for the remainder of the year. If a lag of 2 to 3 months is allowed for the effect of the rain on flowering, the correlation becomes almost perfect (black squares and straight line; the letter before each slash shows the month of rain, that after the slash the month of flowering). On the average, and with this lag, each additional millimetre of rainfall in the month coincides with one more species in blossom.

If the monthly rainfall is 'lagged' by 2 or 3 months as mentioned above, the correlation becomes near-perfect (Fig. 2), with $R = 0.99$, $R^2 = 0.98$, adjusted $R^2 = .97$, and $p = 0.0001$. The equation reads

Flowering native species = 7.43 + 1.04 $\text{rainfall}_{\text{lag 2-3 mo.}}$ (equation 1)

The straight regression line expressed by this equation is rather steep: for every millimetre of rain in a month (lagged) there will be just over one additional plant species in blossom 2 or 3 months later, according to the season.

An interesting question arises: what

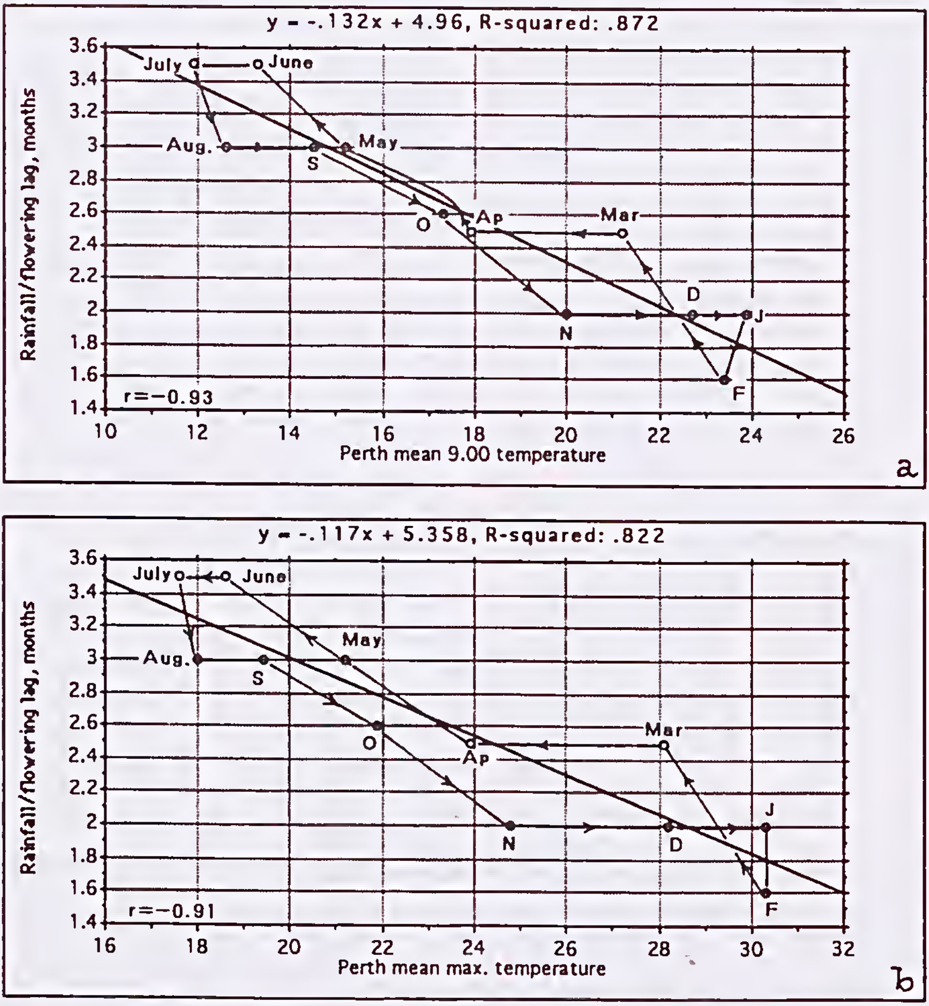

Figure 3. Correlation of (a) mean 9.00 temperature and (b) mean maximum temperature with the lag between rainfall and number of flowering species (as shown in Fig. 2). The higher the temperature, the shorter the lag. A fall in mean monthly temperature of about 6°C would defer the effect of rainfall on blossoming species by about a month.

is the cause of the lag between rainfall and flowering?

THE TEMPERATURE FACTOR

In different climatic regions low temperatures and/or short days and/or inadequate solar radiation slow down, or downright impede, plant functions. In Western Australia daylength and solar radiation are more than adequate for good plant growth, but midwinter has temperatures which are marginally too low. Native plants do not shed their leaves, but their functions are slowed down. The colder it is, the longer it takes for the plant to respond to the beneficial effects of the rain.

In Fig. 3 the lag between rainfall and flowering obtained from Fig. 1 is plotted against two monthly measures of temperature: the mean at 9.00 hours in (a) and the mean daily maximum in (b). The mean temperature at 9.00 hours (Fig. 3a) is most representative of overall thermal conditions because it is not too drastically affected by extreme events such as heat waves or, rarely, frost. The statistical relationship is expressed by

Rain/flowering lag = 4.96 – 0.13 temperature at 9.00 h (equation 2)

with $R = -0.93$, $R^2 = 0.87$, adjusted $R^2 = 0.86$, standard error 0.23, $p = 0.0001$. The greatest discrepancy between graphically estimated and statistically calculated lags is found in March and November, transition months in which climate is very variable and, because of the steep slopes of the graphs in Fig. 1, estimates can only be approximate.

Mean maximum temperatures (Fig. 3b) correlate almost as closely with the extent of the lag for the corresponding months, except for the same transition months of March and November. The equation is

Rainfall/flowering lag = 5.36 – 0.12 mean maximum temp. (equation 3)

with $R = -0.91$, $R^2 = 0.82$, adjusted $R^2 = 0.81$, standard error 0.27, $p = 0.0001$.

ULTRAVIOLET RADIATION

Among the climatic data shown in Fig. 1, ultraviolet radiation (UVR) stands out because of the shape of its curve, which is almost the exact opposite of that for rainfall. This negative coincidence deserves some attention.

Fig. 4 shows that, as was the case with rainfall, in any given month UVR shows no correlation with flowering time. The small circles show the clockwise monthly sequence, and the thin nearly horizontal dashed line the almost non-existent statistical correlation.

If, however, a delay of 3 months is allowed for UVR to have some effect on flowering time, statistical correlation becomes very close indeed, as is shown by the black dots and the parabolic curve in Fig. 4. Correlation would still be very close ($R = -0.91$, adj. $R^2 = 0.82$, SE = 29.99, $p = 0.0001$) if a straight line were fitted, but a parabolic curve shows a near-identity:

flowering native spp. = 309.28 – 21.81 UVR + 0.43 UVR^2 (equation 4)

with $R = -0.99$, $R^2 = 0.97$, adj. $R^2 = 0.97$, SE = 12.33, $p = 0.0001$. A very similar result was also obtained by estimating the time lag from the curves in Fig. 1, as had been done for rainfall.

This negative relationship may give a statistical confirmation to the view

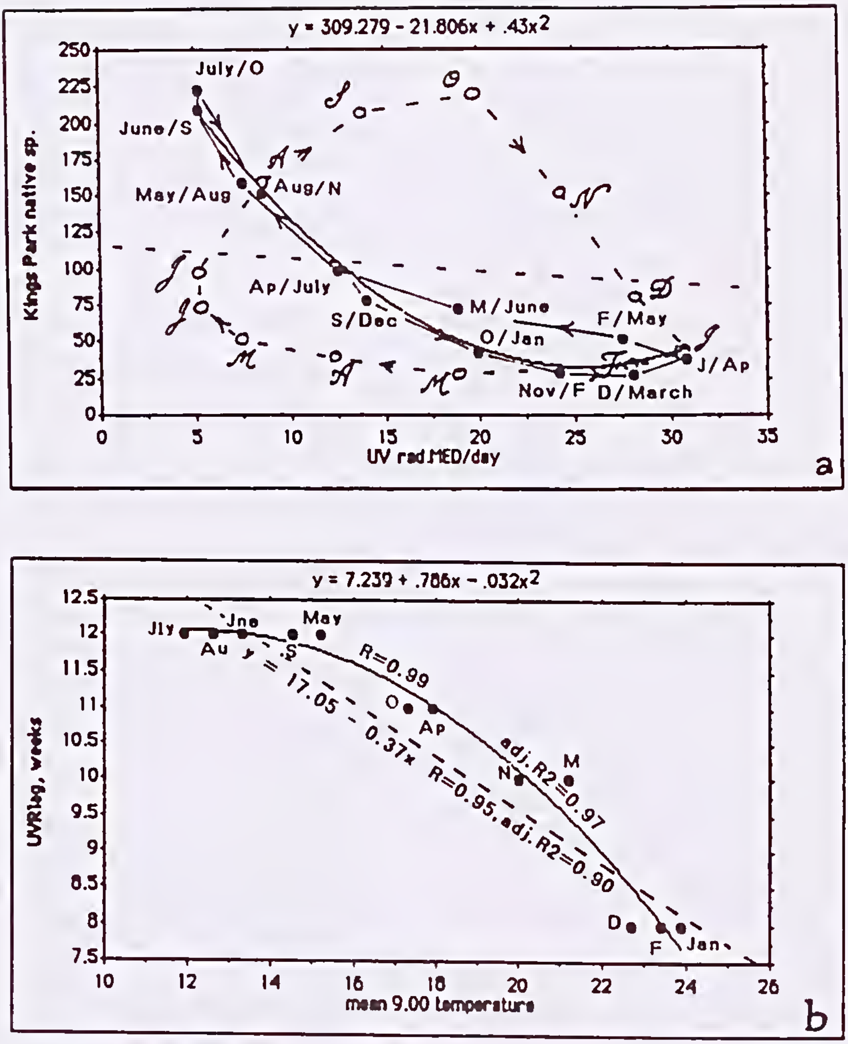

Figure 4. Correlation between ultraviolet radiation and number of flowering native plant species in Kings Park. (a) As in Fig. 2, small circles and cursive letters show the position of each month on the graph, clockwise here because of the negative correlation. If a standard lag of 3 months is applied, each month's UVR correlates with the number of species blossoming 3 months later, hence Nov/ Feb, D/ March...June/ S, etc. with the black dots on the graph. The general trend could be roughly represented by a straight line, but as the graph shows, a parabolic curve gives a most satisfactory image of this very close correlation. As the equation at the top shows, a monthly increase of UVR of a unit per day would coincide with a fall of over 21 species in flower three months later. (b) Correlation between mean 9.00 temperature and lag between UVR values and number of native plants flowering. In this case two refinements have been introduced: lags have been estimated from the graphs in Fig. 1, and have been expressed in weeks instead of months. Cold increases the lag (i.e. defers the effect), heat shortens it. Notice the very rapid changes during the transitional seasons of Spring and Autumn.

that UVR has an inhibiting effect on flowering. The parabolic relationship in equation (4) and Fig. 4 may be seen as another example of acceleration of processes past the equinoxes, and deceleration around the solstices.

REGIONS OF ORIGIN

The regions of origin of naturalised species may be found from various sources, among which most recent and informative for the Perth region are the two volumes by Marchant *et al.* (1984). In the past, unfortunately, the naming of most geographical sources, particularly for early-named species, was far too general: South America was often given as just one area of origin, and yet it is a very large continent with a great variety of latitudinal as well as altitudinal climates. Cape Town has a climate very similar to that of Perth, but in South Africa the rainfall regime changes rapidly towards the east and becomes very similar to that of Queensland, with wet summers and dry winters – and yet all non-South-African publications are content with "South Africa" as one region.

Like Fig. 1, Fig. 5 is also drawn on a semi-logarithmic scale, so that equal rates of change are shown by equal slopes. In the order of their greatest monthly number of flowering species in Kings Park, the regions sufficiently represented are: Europe including Britain (but excluding the Mediterranean region, 46 species flowering in October), South Africa (32 in September), mainland Europe (i.e. excluding Britain and the Mediterranean, 31 in October), the Mediterranean region (16 in October), and South America (7 in October and 7 in November). Most of the species listed in early years as coming from Britain are also found in continental Europe, but very likely their seeds were actually imported from Britain.

The peak of flowering varies little with geographical origin, except for South African plants which in Kings Park blossom a little earlier than plants from elsewhere. The curve showing their time of flowering rises more steeply than any of the others, and the lag of their flowering time persists around 3 months behind the rainfall for most of the year. All in all, their response to rain seems much more direct than occurs in the much larger and varied population of Western Australian native plants; this may be in good part due to the fact that some 20 ot these South African species are equipped with bulbs.

A comparison of climatic data shows that Cape Town is slightly cooler than Perth, particularly in the warmer part of the year, and much drier except in summer.

It may well be that many South African plants are slightly held back by the drier Perth summer, and then respond vigorously to the (for them) unusually plentiful supply of water from March–April onwards, with a minor peak of flowering in May. This interpretation would conflict with the experimental results quoted by Schimper (1898).

Some plants of European origin show a minor peak of flowering in March–April. Perhaps their flowering at that time is influenced by the shortening daylength, as it might well have been in their original home, rather than by rainfall. It is only a small number of species, but this peculiarity makes them interesting, the more so because Western Australian native plants do

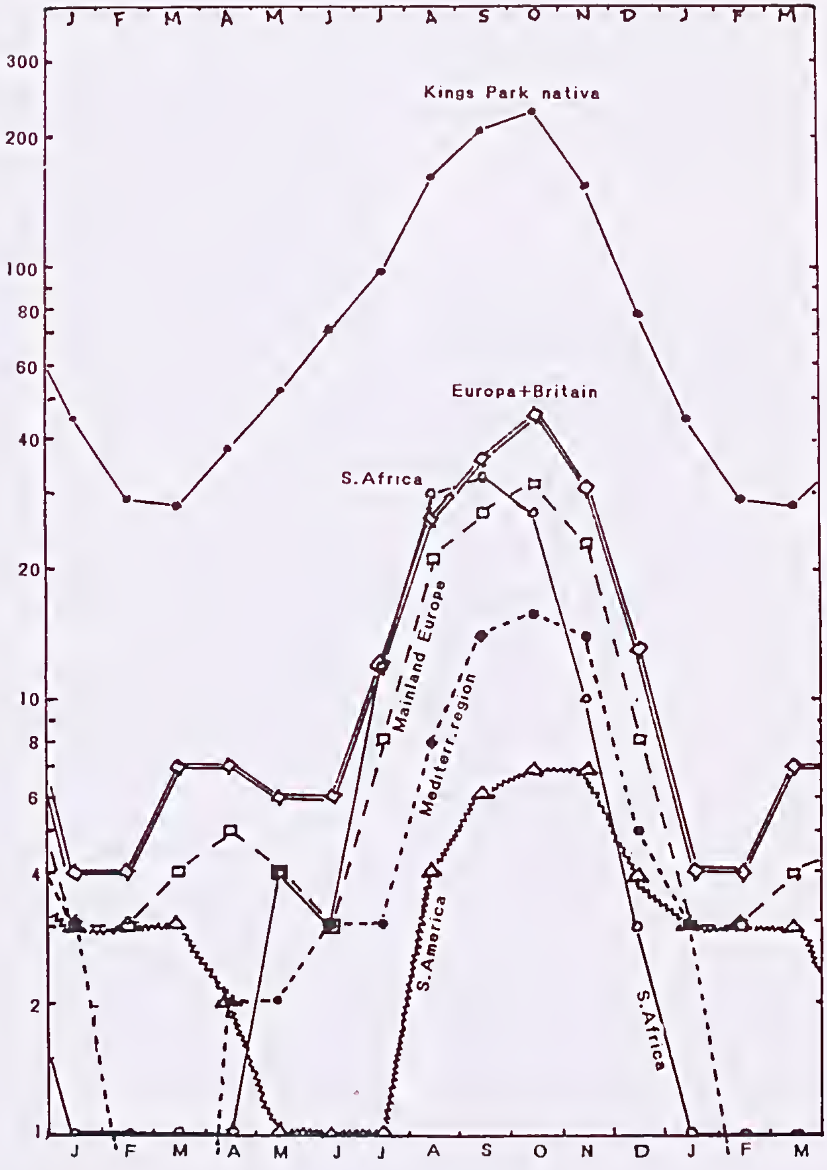

Figure 5. Monthly number of species in blossom in Kings Park, by region of origin. Notice the small but distinct Autumn peak in numbers of flowering plants of European or Mediterranean origin and the less marked irregularities among introduced plants from other continents. In contrast, the graph of native species in blossom is smooth (but compare with Fig. 6, where there is a small Autumn peak). Could the greater differences be due to a genetically set remnant of the effects of Northern Hemisphere Spring? South African plants have 4 species blossoming in May and only 3 in June, and their flowering peak falls early, in September rather than October, but this may be due to various causes as mentioned in the text.

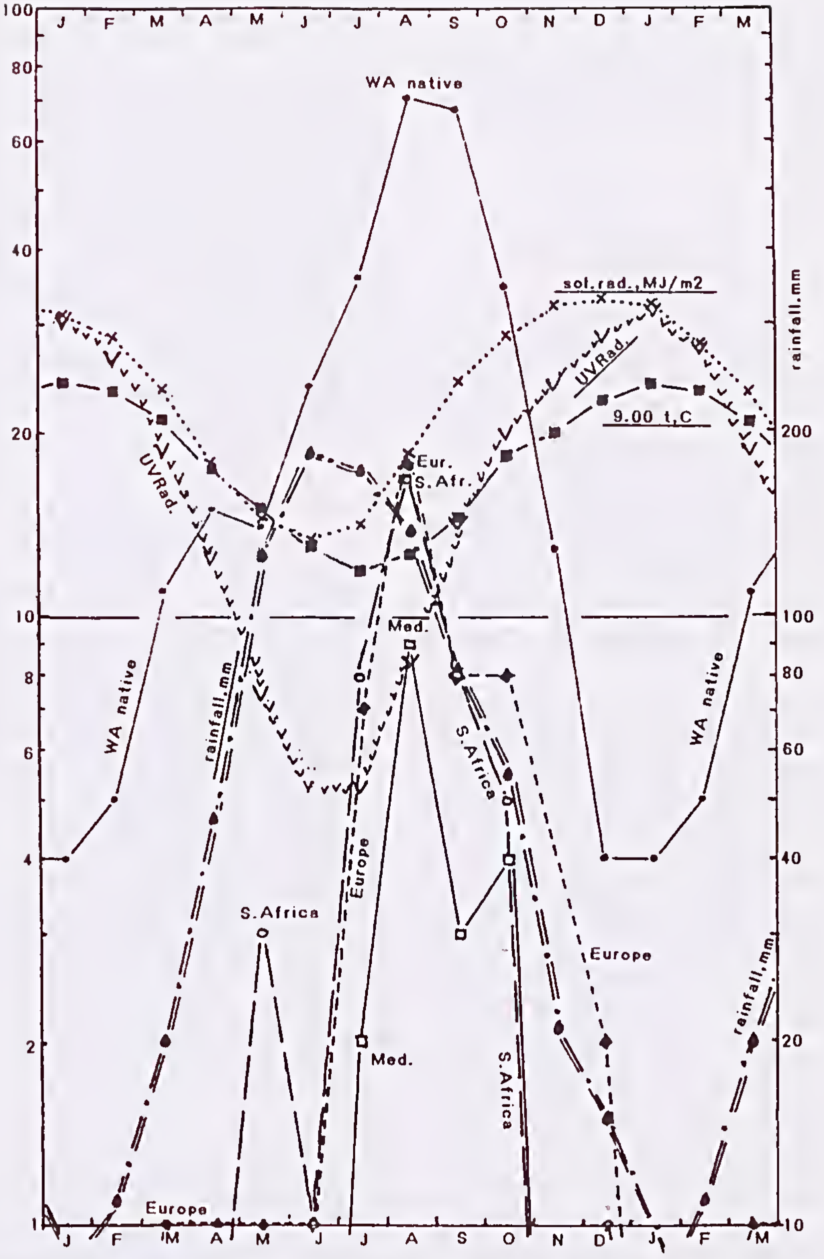

Figure 6. Number of plant species coming into blossom in Kings Park each month, by regions of origin, also rainfall (double dashed line, scale at right) and UVR (VvvvV line, scale at left) All curves are more slender than those of Fig. 5, and their peaks are sharper. Native plants show a minor peak of flowering in March–April, and oversea plants in October. Notice the lag between rainfall and UVR on one hand, and number of species coming into blossom on the other.

not show this habit at all (Fig. 5).

Plants of American origin are too few and their actual ancestral region too uncertain to support any meaningful hypothesis.

THE MONTH OF FIRST FLOWERING

Bennett's and Marshall *et al.*'s studies show that flowering time may last from one to twelve months according to the species, with the majority flowering during two or three months. A distinction should be made between the beginning and the duration of flowering, the latter being influenced by additional factors such as genetics and size of the plant, roots and soil and moisture conditions, flower texture, structure, pollination, etc.

A comparison of Figs. 5 and 6 shows that in the latter the number of species in blossom in any one month is considerably reduced. Graphically, the rises and falls with the seasons appear much steeper. Not only does the April–May minor peak of flowering persist in some naturalised species, but it also appears in April among a few Western Australian native species. Furthermore, an October 'shoulder' appears in the flowering times of naturalised plants. Pending further research, not too much importance should be given to this behaviour of a few species; observations should continue, if possible, over a number of years.

The minor late-autumn peak and the embryo late-spring 'shoulder' hint at some slight setback in the intervening winter flowering. It is usually assumed that this is due to low winter temperatures, but in fact 'the lowering of winter temperatures' is a more meaningful expression. A correlation of any measure of temperature (mean maximum or minimum, wet- or dry-bulb temperature at 9.00 or 15.00 hours) with the estimated 'loss' of flowering in the four coldest months gives correlations above 0.90. Correlation with the amount of low cloud (which is usually dense cloud) gives $R = 0.92$, adj. $R^2 = 0.76$ with $p = 0.08$. These very significant values confirm the desirability of further research into the role of radiation.

FLOWER COLOURS IN THE KALAMUNDA HILLS

Marshall *et al.*'s book does not distinguish the species according to origin (this could be done by consulting Marchant *et al.*, 1984), but there are some interesting data on flower colour. Fig. 7 shows that plants with white-coloured flowers dominate throughout the year, followed very closely by those with yellow and those with red flowers. Between February and April about three times as many red-flowered plants are in blossom than yellow-flowered ones. The slight predominance of yellow over red flowers lasts only during the peak flowering time, from June to early November.

The period with fewest blue-flowering plants in blossom is longer, from February to June. In June there are still only 4 species displaying blue flowers, compared with 38 species with white, 23 with yellow and 21 with red flowers, all nearing their peak. This peak lasts from August to October, while blue-flowered species lag slightly behind, reaching their

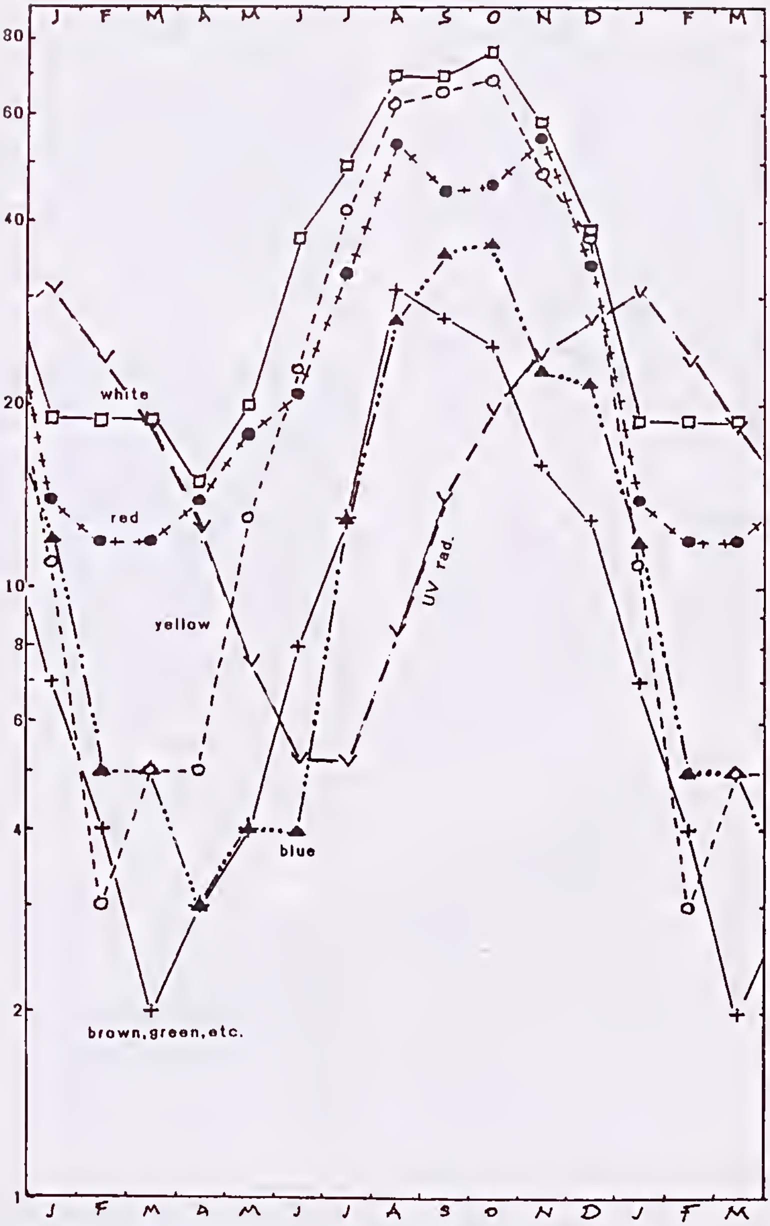

Figure 7. Plant species in blossom in the Hills, by month and flower colour. Notice how red and blue flowering species appear to have slightly different changes of monthly frequency compared with species with flowers of other colours; the September–October decrease in the number of red-flowering species coming into blossom and the post-August decline in brown or green flowers are particularly interesting, and should be investigated. Adaptation to pollinators' behaviour?

distinctly lower peak in September–October. Brown- or green-flowered species show the opposite trend, with an early flowering peak in August.

Red-flowering plants show a peculiarly shaped peak period, with the greatest numbers blossoming in August (54 species) and November (55), but only 45 and 46 species in September and October.

The last group, which includes brown or green flowers, rises faster than any other group to a sharp peak in August, then declines slowly over the following months.

POSSIBLE COLOUR-DIFFERENTIATING FACTORS

If one correlates ultraviolet radiation with the number of flowering species after a 3-month lag one finds remarkably close correlations, irrespective of flower colour (Fig. 8).

The number of yellow-flowering species varies (statistically) very rapidly with changes in UVR: for every additional UVR unit there is an average fall of 2.60 in the number of these species in blossom. The slightly more numerous white-flowering species show a very similar trend, with a fall of 2.39 species for every UVR unit.

The numbers of blossoming species with flowers of other colours, while still varying very closely with UVR (all correlations above 0.90), do so at a slower rate: 1.65 fewer species with red flowers and 1.26 fewer species with blue flowers for every additional UVR unit. The small mixed group of plants with brown, bronze, green, etc. flowers comes last, with a decrease of 1.01 species for any additional UVR unit.

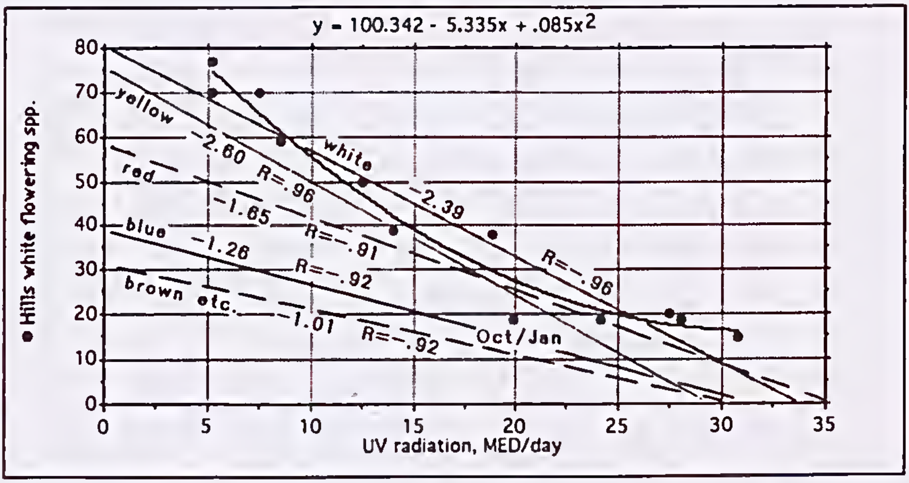

Figure 8. Correlation graph between ultraviolet radiation and number of Hills species in blossom, by colour and allowing for time lag. All correlations exceed 0.90. Correlation for white-flowering plants is shown month by month by the small dots, of which only the Oct/Jan one (October UVR, January flowering) is labelled. The sequence could be represented by a straight line or even better by a parabola (equation at the top). Each line is distinguished by the flower colour, by a small negative number which shows the number flowering species 'lost' for an increase of one unit of UVR, and by the coefficient of correlation R.

Keighery (1996) mentions that bird-pollinated flowers are mostly red or yellow, never blue (for pollination by vertebrates see also Barrett 1995), while most insects are blind to red and thus are not attracted to red flowers. It is logical to expect that UVR affects the pollinators as well as the plants, and its effect on flowering time may be an indirect one..

CONCLUSION

Water, light and warmth are all climatic elements needed for plant life; plants respond most significantly to increases which follow a scarcity of any one of these elements, in Perth's climate the increased rainfall after the summer drought.. However, flowering is the result of complex processes which require some time to develop, and which are affected by the amount of heat available, commonly measured by temperature. The normal lag between rainfall and flowering is about two months, but colder weather retards the effect of increased moisture by a further month.

Northern Hemisphere spring and autumn seem to make some very slight difference to the sequence of flowering among Kings Park's naturalised species, with minor increases which are not found among native species. Among the Hills species, plants with white or yellow flowers respond regularly, after the same delays, to the stimulus of rain. Plants with red or blue flowers show some slight differences in the statistics of their monthly sequences of flowering, and this suggests that some other environmental factor may also be involved.

Monthly values of ultraviolet radiation (UVR) correlate negatively with the numbers of flowering species, and if a lag of three months is allowed, correlate as closely as rainfall, albeit negatively. If the lag is scaled from two months in summer to three months in winter, the negative statistical correlation between UVR and flowering species becomes almost perfect. Can this suggest that UVR is an inhibiting factor, or is all this only an extraordinary coincidence? Some experimental work may decide.

Only phenological observations, over a number of years, may provide a sufficiently detailed and chronologically sound database to allow a really meaningful study of correlations between climatic elements and phases of plant life. It is not enough to be told that, say, 53 species of plants flowered in September, it must be recorded which September it was, and what were its climatic characteristics.

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